THE SKULL AND MANDIBLE OF A NEW CISTECEPHALID DICYNODONT

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(With 4 figures)

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Introduction

The dicynodont genus *Cistecephalus* is one of the more well-known groups of South African therapsids, and its unusual, readily identifiable skull form and stratigraphically limited occurrence (Keyser 1965; Kitching 1970) make it a valuable marker genus in the Beaufort Series zoning system. Several species (11) have to date been described but reviews of the genus have shown that only 9 of these are in fact based on specimens of *Cistecephalus*. These are *C. microrhinus*, *chelydroides*, *planiceps* and *bathygnathus* (Owen 1876); *angusticeps* (Broom 1932); *major*, *rubidgei* and *platyfrons* (Broom 1948) and *laticeps* (Brink 1950). Several synonymies have at various times been declared among these species (see Brink 1950; Keyser 1965); in the most recent review, Keyser (1965) recognizes only *C. microrhinus* Owen but at the same time has found evidence for a new species.

Cox (1972) has recently described a new East African dicynodont, *Kawingasaurus fossilis*, which he states is fairly closely related to *Cistecephalus* but has important differences in the skull and especially the postcranial skeleton.

The specimen at present under discussion (SAM 6243) could at first glance be regarded as a species of *Cistecephalus* with somewhat unusual skull proportions, but removal of the lower jaw and exposure of the palate and basicranium revealed a basic skull structure which differs widely from the *Cistecephalus* and, indeed, the standard dicynodont condition. These differences

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appear to warrant generic distinction, and are summarized in the following section.

Classification

The creation of a new genus, closely allied to *Cistecephalus*, raises the question of the status of *Cistecephalus* itself. Although the recent classification of Romer (1966) places the genus in the family Dicynodontidae, earlier workers tended to emphasize the unusual skull structure of the genus by setting it apart from other dicynodonts. Thus Seeley (1894) was led by the unusual skull roof (the palate was at that stage unknown) to regard the genus as being sufficiently far removed from his suborder Dicynodontia to warrant a separate suborder, Kistecephalia. Most subsequent authors have, however, been content to leave the genus in a separate family. Broom in 1903 proposed a family Cistecephalidae for the genus, distinct from the Endothiodontidae, Dicynodontidae and Lystrosauridae, and distinguished from these by the structure of the quadrate and occipital regions. Broili & Schröder (1935: 17) found additional grounds for maintaining this family, which they diagnosed as:

> 'Skull short-snouted, relatively high, intertemporal width greater than interorbital width, no preparietal, no independent postfrontal and probably no tabulars, and also no interpterygoidal opening. Toothless.'

Haughton & Brink (1954: 69) have retained the family Cistecephalidae, which they define as having:

> 'Small broad skull. Molarless. Very wide and flat intertemporal region.'

Investigations into the anatomy of *Cistecephalus* undertaken for the purposes of the present work make it clear that the genus's strikingly unusual cranial structure demands familial distinction, on the lines proposed by Broili & Schröder (1935) and Haughton & Brink (1954). The pertinent cranial characters of the family and genus, and the relationships of Cox's *Kawingasaurus* and the proposed new genus and species, may be formalized as follows:

Class **REPTILIA**

Order THERAPSIDA

Suborder ANOMODONTIA (*sensu* Romer, 1966)

Infraorder DICYNODONTIA (*sensu* Romer, 1966)

Family **Cistecephalidae** Broom, 1903

Diagnosis: Small, toothless dicynodonts with very broad intertemporal region, lacking a preparietal and postfrontal. Squamosal not extended posteriorly beyond level of the supraoccipital; stapes perforated or deeply incised; interpterygoidal vacuity vestigial or absent.

Genus *Cistecephalus* Owen, 1876

Diagnosis: Cistecephalids with broad or narrow interorbital region. Lacrimal foramen absent or low down within orbit; pterygoids meeting below parabasisphenoid complex; interpterygoidal vacuity absent.

Genus *Kawingasaurus* Cox, 1972

Diagnosis: Cistecephalids with moderately broad interorbital region and relatively small orbits. Postorbital and prefrontal separated by frontal. Lacrimal foramen in normal dicynodont position, pineal foramen absent. Zygomatic arch slender. Stapedial foramen present and interpterygoidal vacuity absent.

Genus ***Cistecephaloides*** gen. nov.

Diagnosis: Cistecephalids with broad intertemporal and interorbital regions, reduced orbits and robust postorbital bars. Prefrontal meeting postorbital, lacrimal foramen in usual dicynodont position; stapes deeply incised and reduced to slender bar; pterygoids extending far backwards onto basioccipital tubera, separated in midline by parasphenoidal rostrum which runs forward in palatal view to meet vomer. Interpterygoidal vacuity represented by small fossae (possibly foramina) alongside parasphenoid. Dorsal dentary surface of jaw ramus drawn up laterally as a sharp, longitudinal blade.

Cistecephaloides boonstrai sp. nov.

Diagnosis: as for genus.

Holotype: SAM 6243. Partially weathered skull and mandible.

Locality: Ely Cottage, near Alice, Cape Province, South Africa.

Horizon: Cistecephalus zone (*Daptocephalus* zone of Kitching, 1972) of Upper Permian Middle Beaufort Series.

I have pleasure in naming the new species after Dr L. D. Boonstra, who introduced me to vertebrate palaeontology.

Haughton & Brink (1954) include the genus *Emydorhinus* Broom under their Cistecephalidae, but, with the exception of the loss of the postfrontal, there do not appear to be any significant resemblances between this genus and *Cistecephalus*, *Kawingasaurus* and *Cistecephaloides*.

Cranial Morphology of *Cistecephaloides boonstrai*

SKULL

The skull lacks the left zygomatic arch, the right quadrate and otic region, and a portion of the skull roof above the left temporal fossa. In addition, the left cheek region and the adjoining palatal surface is incomplete, while in ventral view the anterior portion of the palate and basicranium is displaced dorsally at a shear just anterior to the level of the internal carotid artery canals. These imperfections are relatively easily compensated for, and the illustrations of the reconstructed skull may be regarded as being reasonably accurate.

The skull shows the usual cistecephalid proportions and is triangular in dorsal view, being widest over the rear of the squamosals. In the actual specimen, before allowance is made for distortion, the width of the skull over this region is 58 mm, as compared with the basioccipital-premaxilla skull length of

61 mm. In the reconstructed skull, these measurements become respectively 63 and 62 mm.

Snout and skull roof

The edges of the palatal rim are lacking, and the ventral limits of the snout are thus difficult to determine. On the more complete right-hand side the maxilla is flared out laterally in front of the orbit to form a prominent and robust ledge, which lies as a forward prolongation of the zygomatic arch. The septomaxilla is exposed on the surface of the snout behind the external naris, and forms a small part of the floor of the anterior nasal chamber. Behind the septomaxilla the maxilla rises up high in the side of the snout to meet the nasal.

The nasal covers a relatively large area on the snout and skull roof, and forms a small boss over the external naris. Anteriorly, in the region of the external naris, the nasal is perforated by numerous nutritive foramina and channels.

The small size of the orbit is one of the striking features of the skull. The postorbital bar is a robust pillar, and the bone extends forward above the orbit to make contact with the prefrontal, thereby excluding the frontal from the orbital border. The lacrimal and prefrontal have little exposure on the lateral snout surface, but the lacrimal forms a large part of the inner wall of the orbit, and is pierced by a foramen for the duct of the lacrimal gland in the anteroventral corner of the orbit, in the normal dicynodont position. The prefrontal forms only the anterior half of the inner orbital border, and behind it the lacrimal makes contact with a forward extension of the frontal.

The maxilla does not reach far back on the zygomatic arch, and the jugal, extending out from below the lacrimal inside the orbit, forms the major part of the infraorbital bar.

The intertemporal part of the skull roof is weathered and discoloured, and sutures are consequently difficult to trace. The frontonasal suture is clear, and extends back to the level of the rear of the orbits. This level is well within the rear half of the skull, and accordingly the frontals and parietals are short, wide elements. A frontoparietal suture can be distinguished near the midline of the skull, while traces of a parietal-interparietal contact can be seen on the rear edge of the skull table. From these it appears that the frontals are considerably shorter than the nasals, while the parietals, shortest of all, are confined to the extreme rear of the skull roof. Laterally each parietal passes forward for a short distance, between the postorbital and frontal of its side. An inner flange of the frontal passes forward and down medially to the postorbital to form part of the inner wall of the orbit, where it meets the prefrontal and lacrimal. A similar but more vertical flange of the parietal forms the median wall of the temporal chamber and meets the dorsal tip of the epipterygoid.

No clear parietal foramen can be made out, but a circular, damaged area in the midline of the skull in the parietal region has within it portions of smooth,

vertically standing bone, which may represent part of the pineal canal. In any event, the parietal foramen, if present, could not have been more than a small, relatively insignificant opening.

Occipital region

As in *Cistecephalus*, the squamosals in *Cistecephaloides* do not extend back beyond supraoccipital level, and the occiput (Fig. 4) is thus an open and slightly rounded surface, the occipital condyle being the most posterior structure. From the condyle the occiput slopes forward fairly steeply, so that the plane of the occiput meets that of the skull roof at an angle slightly in excess of 90°.

Considerable damage to the occipital region has been caused through weathering, and some doubt exists as to the exact relationships held between supraoccipital, interparietal and squamosal, especially in the dorsal part of the occiput. In addition, the presence or absence of a tabular is open to question. The interparietal forms a low nuchal crest immediately behind its meeting with the parietal and extends down and laterally on the occiput to meet the supraoccipital and squamosal. Both supraoccipital and interparietal slope back towards the exoccipital, the condyle of which lies in the most posterior plane of the skull. Medially the exoccipital carries a short, blunt process for the proatlas on the margin of the foramen magnum, and laterally it terminates in the inner corner of the posttemporal fossa. Above the condyle it forms the posterior wall of the jugular foramen.

Because of the considerable lateral extent of the exoccipital, the opisthotic does not make any contact with the supraoccipital on the occipital surface. From the posttemporal fenestra the opisthotic-squamosal suture is deeply interdigitated and runs ventrolaterally, but the meeting lower down between the squamosal and the lateral paroccipital process is, in contrast, a fairly loose one. Ventrolaterally (Figs 1, 3, 4) the opisthotic bears a sharp crest which is drawn out posteriorly as a fairly prominent 'opisthotic' process, the equivalent of the tympanic process of Cox (1959). Below this is the channel for the lateral head vein, narrower than in other dicynodonts, and deeply incised into the opisthotic's ventral border.

The dorsal extent of the squamosal is uncertain, but below its meeting with the postorbital it forms an extensive sheet-like border to the occiput; in common with species of *Cistecephalus*, this occipital part of the squamosal is flat and lacks the posterior flanges found in other dicynodont groups.

The occipital condyle is the most posterior part of the skull. The lower half is formed by the basioccipital, while the two exoccipitals complete the structure dorsally. The exoccipital part of the condyle does not project back farther than the basioccipital part, as is the case in some dicynodonts, and, since the basioccipital and exoccipitals are depressed to form a notochordal pit in the centre of the condyle, the actual articular surface is a flat, ring-shaped area.

The quadrate and quadratojugal hold the normal dicynodont relation-

ships with each other. Ventrally the quadratojugal is indistinguishably fused with the dorsal surface of the lateral quadrate condyle, but dorsally its suture with the squamosal is clearly visible above the quadrate foramen, where the quadratojugal and quadrate are separated by a ventral process of the squamosal.

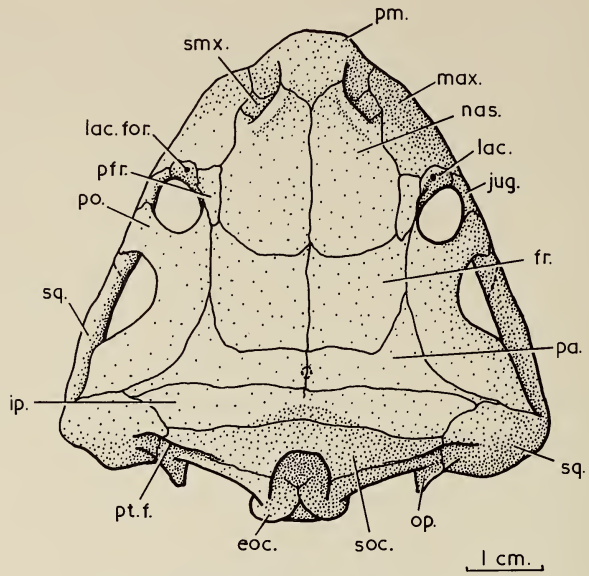

Fig. 1. *Cistecephaloides boonstrai* gen. et sp. nov.
Skull in dorsal view. Natural size.

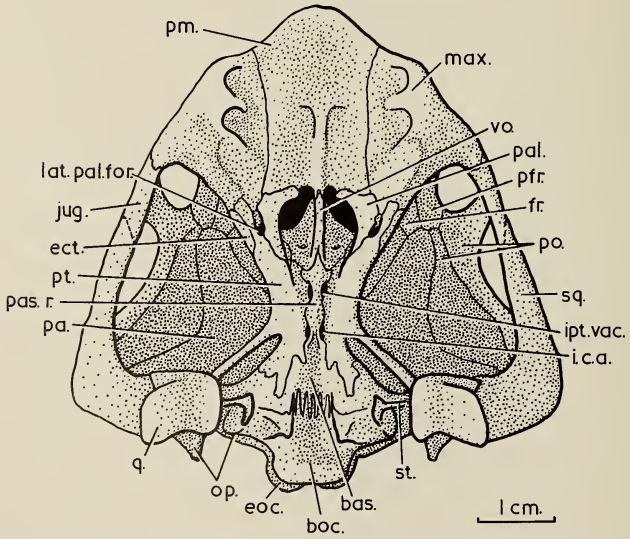

Fig. 2. *Cistecephaloides boonstrai* gen. et sp. nov.
Skull in ventral view. Natural size.

The articular surface of the quadrate has the form of a wide trough, dorsally curved anteriorly and posteriorly, and is not easily divided into distinct lateral and medial condyles. The major part of the articular area faces forwards and down, but at the rear this surface curves sharply upwards to meet the ventral edge of the squamosal.

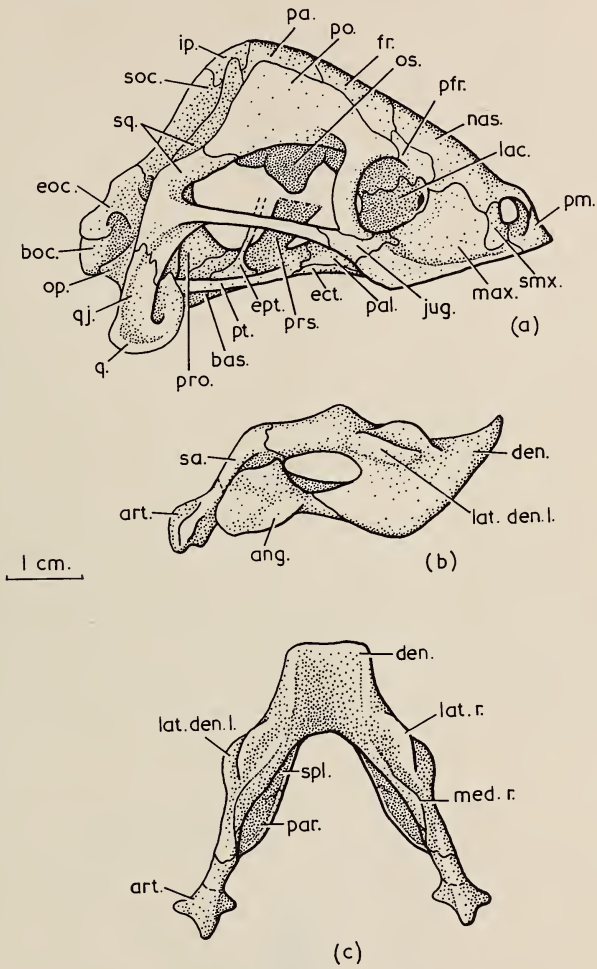

Fig. 3. *Cistecephaloides boonstrai* gen. et sp. nov.
(*a*) Skull in lateral view. (*b*) Mandible in lateral view. (*c*) Mandible in dorsal view. Natural size.

Basicranial axis and palate

The basioccipital-basisphenoidal tubera are prominent features in the ventral part of the braincase, and their structure can be fairly accurately determined in the more complete left-hand side. The rear of the tuber is widely

excavated over the basioccipital-basisphenoid suture, and it is possible that this part, which is unfinished in periosteum, was completed in cartilage during life. Above this area, the opisthotic is flared backwards as a slightly concave, horizontal ledge, below and lateral to the opening of the jugular foramen.

In the ventral midline the highly interdigitating basioccipital-basisphenoid suture is clearly visible. The suture straightens out on the inner side of each tuber, but weathering on these ventralmost points in the skull obscures the meeting between basioccipital and basisphenoid in the region of the fenestra ovalis. Interpretation of this area is further complicated by the unfinished, porous nature of the bone surface, suggesting that the rim of the fenestra ovalis was at least partly formed in cartilage.

The stapes itself appears to have been partly cartilaginous. A fairly substantial footplate is present, but the body of the element is represented only by a very thin bony splint, arising from the anterior end of the footplate and not quite reaching the quadrate. As such, the stapes is an extremely light and delicate structure, and the considerable posterior extent of the footplate, finished in periosteum, suggests that the bone was deeply notched, possibly to allow passage for the stapedial artery and chorda tympani nerve. The distal end of the stapes, which normally abuts against the inner side of the quadrate condyle, is not preserved, and during life was probably present as cartilage.

On the anterior slope of the basioccipital tuber the basisphenoid is overlain by a long, irregular posterior extension of the pterygoid, which reaches back almost to the level of the fenestra ovalis. In front of the meeting between the body of the pterygoid with the quadrate ramus, the basicranial girder is sheared through, and the anterior portion displaced dorsally, but in spite of this complication it is possible to make out the relations which the various bones hold with each other. Most striking is the lack of contact between the pterygoids in the ventral midline. In front of the internal carotid artery foramina

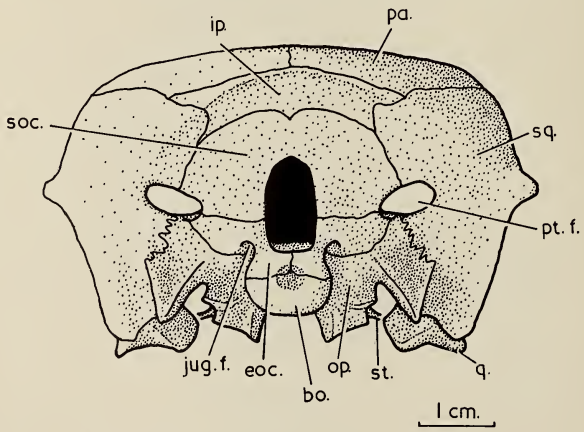

Fig. 4. *Cistecephaloides boonstrai* gen. et sp. nov.
Skull in posterior view. Natural size.

the pterygoids approach each other, but are clearly separated by an anterior extension of the parabasisphenoid complex. Anterior to this, the pterygoids diverge to form the lateral borders of the internal choanae, and a pair of deep recesses are formed between the pterygoid and the median, parabasisphenoid bar. These recesses are apparently vestiges of the interpterygoidal vacuity which is found in other dicynodonts (except *Cistecephalus*). The lateral borders of the choana, formed by pterygoids, palatines and ectopterygoids, are criss-crossed by a network of small cracks, and sutures are thus difficult to determine with complete certainty. It seems, though, that each pterygoid extends forward to make a short contact with the maxilla and, together with the palatine and a posterior process of the premaxilla, closes off a large lateral palatal foramen at the level of the anterior part of the choana. In this region the pterygoid is wedged between the palatine medially and the ectopterygoid laterally.

The palatine has a limited palatal portion and the major part of the bone lies as a low outer wall of the choanal passage. Posteriorly this palatine wall makes contact with an anterior extension of the parabasisphenoid complex laterally, and with the vomer medially, where this latter bone curves outwards to form the posterior wall of the choanal passage. Anteriorly the palatine passes forward to the ventral part of the orbital wall, where an anterior lappet meets the lacrimal and jugal.

The ectopterygoid is a thin splint of bone lying entirely lateral to the anterior part of the pterygoid. It makes contact with the maxilla but does not border onto the lateral palatal foramen. The vomer, on the other hand, is an important bone in the palate and lies as a deep and stout median septum which descends to the level of the lateral, pterygoidal borders of the choana, effectively separating the two internal nares from each other. Dorsally the septum widens as the vomer curves out on each side to form a partial median roof for the choanal passage, the roof becoming complete at the meeting of the vomer with the palatine at the rear of the choana. Anteriorly the vomer is clasped by a pair of diverging processes of the premaxilla, while posteriorly it, in turn, contains the anterior parasphenoidal prolongation of the parabasisphenoid.

The bony secondary palate, formed by premaxilla and maxilla, is wide and bounded by a low palatal rim. On either side of its median palatal ridge (a functional continuation of the parasphenoid-vomer bar), the premaxilla slopes away to form a pair of shallow recesses, which merge in front of the median ridge to create a vaulted area behind the anterior palatal rim. Medial to the lateral palatal rim, along the maxilla-premaxilla suture, the palate is raised as a narrow ledge, which terminates anteriorly as a weak lateral palatal ridge on the premaxillary palatal rim. The palatal rim itself is damaged on both sides of the snout, but it is nevertheless apparent that the rim was thin and sharp-edged anteriorly, while posteriorly it probably became more robust near the short, blunt caniniform process. The posterior, maxillary portion of the palatal rim is medially scalloped, and two embayments lead onto the lateral palatal ledge. The posterior of these is the more pronounced, and lies

anterior to a smooth, concave portion of the maxilla which slopes postero-medially from the caniniform process to merge with the palatal surface level with the anterior margin of the choana.

Temporal region

The left side of the skull has been completely cleared of matrix and portions of the braincase and basicranial axis have been exposed. The prootic-basisphenoid suture is clear, and a small depression, half-way along its length, leads to the foramen for the exit of the facial nerve. There is no deep sulcus in the prootic in front of the posttemporal fenestra, such as is found in many other dicynodonts and which appears to have stood in connection with the venous system of the head (Cox 1959; Cluver 1971), and no notch (venous notch of Agnew 1959) is found between the prootic and parietal in the sidewall of the braincase.

The braincase lies deep within the greatly enlarged temporal vault. Frontal, postorbital and parietal combine to make an extensive roof behind the orbit, and the temporal fenestra opens almost entirely laterally, the roofed-over area being best developed posteriorly, where the skull roof joins the occipital plate. The bone forming the temporal roof is uniformly thin, but above the temporal fenestra the ventral border of the postorbital is inflated to a powerful, bar-like rim, which extends from behind and medial to the postorbital bar to the posterolateral corner of the temporal fenestra (Fig. 2).

In front of the hypophyseal region the basisphenoid lies as a horizontal sheet, meeting the pterygoids laterally and the palatine anteriorly, and carrying the presphenoid dorsally. A notch visible in lateral view between the basisphenoid and the anteroventral edge of the presphenoid lies above the pair of deep fossae in the palate which represent the vestigial interpterygoidal vacuity. In typical dicynodonts a similar notch serves as the dorsal opening of the interpterygoidal vacuity, and although it is reduced in *Cistecephaloides*, its presence suggests that the interpterygoidal openings might in fact pass upwards to open out above the pterygoids, a condition which has been lost in *Cistecephalus*. Verification of this possibility by further preparation was, however, prevented by the delicate nature of the bones in this region of the skull.

As stated earlier, the rear of the palate in the type specimen has been displaced upwards at the level of the internal carotid artery canals, and the presphenoid is consequently partly concealed behind a sheet of bone descending from the skull roof. This bone (os, Fig. 3), wedged between the descending laminae of the parietal and frontal, appears to be part of a damaged orbitosphenoid complex. Few details can be made out, but it is clear that it forms a considerable part of the upper sidewall of the braincase, and is slightly curved. There is no clear division of the element into a dorsal trough-like portion and a ventral keel.

A small portion of the epipterygoid footplate, in front of the ascending shaft, is present on the dorsolateral edge of the pterygoid, but the major part

of the bone was apparently damaged by the displacement of the palate, and is only partially preserved. Dorsally a lappet of the parietal, descending to meet the upper extremity of the epipterygoid, can be distinguished.

LOWER JAW

The mandible is short and deep in its overall dimensions. The powerful dentaries are completely fused in the symphyseal region and carry a sharp, transverse cutting edge anteriorly. Behind this blade the dentaries are scooped out as a wide trough, and no dentary tables, as found in dicynodonts such as *Lystrosaurus* (Crompton & Hotton 1967; Cluver 1971), are present. Behind the symphyseal region, however, the dorsal edge of the dentary widens, and a wide, shallow dentary groove is formed. The medial wall of this groove rises posteriorly as a sharp blade (med.r., Fig. 3c) forming the medial edge of the dorsal dentary surface. Below this sharp edge the inner surface of the dentary is slightly concave, so that the Meckelian sulcus in the prearticular is exposed in dorsal view. The lateral wall of the dorsal dentary groove, on the other hand, is highest anteriorly, where it rises as a sharp, delicate cutting edge (lat.r., Fig. 3c). Below and lateral to this the dentary is expanded above the mandibular fenestra to form a robust lateral dentary ledge. Below the large mandibular fenestra the dentary passes back to meet the angular.

The dorsal, surangular margin of the jaw curves down steeply, and the articular is consequently carried relatively low in the mandible; this feature may, however, be partly the result of distortion which the mandible appears to have undergone. The main articular condyle is a wide, slightly concave facet, while a smaller median facet is carried on a delicate inner ledge. The two surfaces are separated by a rounded and ventrally curved longitudinal ridge. The ventral extremity of the articular, together with any evidence of a retroarticular process, has been lost through weathering.

The medial border of the Meckelian sulcus is formed by the prearticular posteriorly and the splenial anteriorly. As stated earlier, the inner surface of the dentary above the sulcus is hollowed out, and a wide, smooth depression leads down anteroventrally into the trough.

Comparison with *Cistecephalus* and *Kawingasaurus*

A number of skull features, notably in the skull roof, occiput and palate, indicate that the affinities of *Cistecephaloides* lie more with *Cistecephalus* and *Kawingasaurus* than any other dicynodont genera. The broad intertemporal region in *Cistecephaloides* is (as in *Cistecephalus*) composed of the very wide frontals and parietals, which on each side meet the sheet-like postorbitals. In *Cistecephaloides*, however, an additional feature is the enlargement of the nasals, which extend farther laterally and posteriorly than in any *Cistecephalus* species. Their lateral extent is reflected in the small size of the orbits, while their posterior borders are well within the rear half of the skull. The frontals and parietals are consequently confined to a relatively short and wide area of the skull roof.

The parietals in *Cistecephaloides* do not pass forward between the frontals in the midline, as they do in *Cistecephalus*, but laterally each parietal curves forward between the frontal and postorbital of its side. In dorsal view, therefore, the parietals together cover an open, horseshoe-shaped area on the skull roof, in contrast to the triangular area common in *Cistecephalus*. The fronto-parietal suture is not shown in Cox's (1972) illustrations of *Kawingasaurus*.

The enlargement of the nasal in *Cistecephaloides* and the accompanying increase in the interorbital width and reduction in orbit size have resulted in crowding together of the circumorbital bones and an unusual meeting of the prefrontal with the postorbital above the orbit. The frontal is thereby excluded from the orbital border, but, passing down medially to the prefrontal and postorbital, still forms part of the inner wall of the orbit. Although a prefrontal-postorbital contact does not occur in *Cistecephalus*, these bones do approach each other in some species (*C. planiceps* of Broili & Schröder 1935; *C. laticeps* of Brink 1950), and an anterior extension of the postorbital seems to be characteristic of the genus.

The roofing-over of the intertemporal region in *Cistecephaloides* has been accompanied, as in *Cistecephalus* and *Kawingasaurus*, by the loss of the posterior flange of the squamosal, so that the occiput is an open, slightly convex surface and totally unlike that of other dicynodonts. Apparently related to this modification of the squamosal is the relatively low position of the zygomatic arch in the skull of both *Cistecephalus* and *Cistecephaloides*.

In the basicranium and palate similarities between *Cistecephalus* and *Cistecephaloides* are fewer, although some features appear to parallel each other functionally. Thus an apparent tendency in both genera to strengthen the basicranial girder (connecting the palate with the floor of the braincase) by the reduction or loss of the interpterygoidal vacuity has been accomplished in two different ways. In *Cistecephalus* the pterygoids meet in the midline in front of the internal carotid artery foramina in normal dicynodont fashion, but this contact is strengthened anteriorly by medial pterygoidal extensions which meet the rear end of the vomer, completely obliterating the interpterygoidal vacuity. In at least one species of *Cistecephalus* (*C. microrhinus* of Keyser 1965) a small area of parabasisphenoid complex is still visible in ventral view in the midline between the pterygoids and vomer. Cox (1972) has not given a detailed illustration of this region in *Kawingasaurus*, but states that the interpterygoidal vacuity is absent, and from the drawings it appears that the pterygoids meet in the midline as in *Cistecephalus*.

In *Cistecephaloides*, on the other hand, the pterygoids have parted in the ventral midline but have improved their attachment to the basicranium by developing extensive posterior processes which overlap the basisphenoid to the level of the fenestra ovalis. The parabasisphenoid lies exposed in ventral view between the pterygoids, and the parasphenoid rostrum, which in dicynodonts is usually clasped by the vomers above palatal level (cf. *Lystrosaurus*, Cluver 1971) lies low down in the palate and is clasped by posterior diverging wings of the

vomer to form part of the median septum separating the internal nares.

The parting of the pterygoids has caused the basicranial girder of *Cistecephaloides* to become unusually wide, and this may be associated with the very broad and shallow secondary palate, formed by the maxillae and premaxilla. A second result of the pterygoidal separation is the apparently incomplete closure of the interpterygoidal vacuity, since the pair of deep fossae in front of the internal carotid artery foramina, and in the position of the primitive interpterygoidal opening, may possibly lead to foramina which open out in front of the presphenoid above the level of the pterygoids.

In both *Cistecephalus* and *Cistecephaloides* the vomer lies as a low, stout septum within the choana and, meeting either the pterygoid (*Cistecephalus*) or the basisphenoid complex (*Cistecephaloides*) posteriorly, acts as a median strut between the palate and basicranium.

Several similarities in the palate of *Cistecephalus* and *Cistecephaloides* also exist. In both, the trough-shaped central portion of the premaxilla, which is divided by the median palatal ridge, is separated from the palatal rim by a lateral maxillary ledge, while the anterior part of the palatal rim lacks the anterior palatal ridges which are found in many dicynodonts. Also in both genera, the palatine meets the premaxilla anteriorly, so that the maxilla is excluded from the choana. However, in *Cistecephaloides* the ectopterygoid is reduced to a thin, lateral splint of bone, unlike the relatively large ectopterygoid of *Cistecephalus* and *Kawingasaurus*. Associated with the small ectopterygoid in *Cistecephaloides* is the unusual forward extension of the pterygoid, which meets the maxilla laterally to the lateral palatal foramen.

Both *Cistecephaloides* and *Kawingasaurus* lack the two curious circular depressions in the caniniform process region of *Cistecephalus*, one medial to and the other lateral to the palatal rim. In *Cistecephaloides*, instead, the palatal rim is notched medially in two places at the caniniform process, the posterior notch being the larger and in the position of the inner circular depression found in *Cistecephalus*. *Kawingasaurus* represents a third type, as Cox (1972) states that the palate is unusually flat, and lacks sharp cutting edges.

The structure of the mandible in *Cistecephalus* and *Cistecephaloides* is basically the same. The dentary is widely excavated in the symphyseal region behind the transverse anterior cutting edge, and the dorsal dentary surface of each jaw ramus bears a pair of ridges (more pronounced and sharp in *Cistecephaloides*). Above the mandibular fenestra a distinct lateral dentary shelf is present. Comparisons with *Kawingasaurus* are difficult, as the symphyseal region is incompletely preserved, but Cox's (1972) drawings suggest a low, blunt symphysis, and it seems unlikely that an upright, anterior cutting blade, such as in *Cistecephaloides*, could have been present. All three genera, however, resemble each other in that the dorsal, dentary part of the jaw ramus is bowed out laterally so that the Meckelian sulcus is exposed in dorsal view.

From these comparisons, it appears that *Cistecephaloides*, *Cistecephalus* and *Kawingasaurus* all fulfilled certain common functional requirements but, by

following slightly different, parallel pathways, arrived at their general adaptational level with considerable differences in their cranial structure.

Functional Considerations

The unusual skull morphology of *Cistecephalus* has prompted a number of workers to speculate on the most likely mode of life common to the various species of the genus. The possibility of an aquatic or semi-aquatic way of life was mentioned by Broom (1948) and Brink (1950), but Brink in 1952 described the left manus of a specimen of *C. microrhinus* which, he suggested, indicated a burrowing existence. Brink was led to this opinion by the fusion of the distal phalanges in the 2nd and 3rd digits, and the degeneration of the 1st, 4th and 5th digits. According to Brink the hand had only two powerful, functional fingers, and was thus well adapted for fossorial or burrowing habits.

Keyser (1965) argued that Brink (1952) had misinterpreted his specimen, stating that the digital formula in additional specimens of *Cistecephalus* was of the standard therapsid type, although the two distal phalanges of the 3rd and 4th digits were fused, strongly developed and elongate, and were probably equipped with strong claws during life. In addition, Keyser maintained that the 4th and 5th digits could probably appose the 1st, 2nd and 3rd digits, so that the hand was of the grasping type. Keyser concluded that these features, taken together with indications of stereoscopic vision (such as the large, anteriorly directed orbits) were strongly suggestive of arboreal activities.

Cox (1972) has interpreted the unusual pectoral girdle, humerus and forelimb of *Kawingasaurus* as being adapted for powerful digging, and suggests that the animal might have rooted in mudflats in search of small invertebrates. As stated by Cox, this view is supported by the absence of sharp 'herbivore' cutting edges which form the palatal rim in other dicynodonts.

The skull of *Cistecephaloides boonstrai* does not in itself offer conclusive evidence in support, or otherwise, of any of these theories, but a consideration of the three obviously related genera does to an extent reveal that several of their specializations are the consequence of broadly similar functional requirements. Thus it could be argued that the reduction and loss in all three genera of the interpterygoidal vacuity, together with the increase in thickness and vertical extent of the vomerine septum, represent strengthening of the basicranial axis of the skull to withstand fore-and-aft stress. Again, the broadly roofed-over intertemporal region strengthens the overall skull structure, but this feature of the cistecephalids has an important corollary, and may not have arisen as a purely reinforcing device. Thus, the relatively lateral position of the cistecephalid temporal fenestra, a direct consequence of the broadened intertemporal region, must have brought about considerable changes in the jaw adductor musculature, the deep part of which arose from the bones surrounding the fenestra. Crompton & Hotton (1967) have reconstructed this muscle, the external adductor muscle, in dicynodonts, and suggest the dorsal surface of the postorbital and posterior flange of the squamosal (being respectively the

medial and posterior margins of the fenestra) as the most likely areas of origin. The moulding of these bones in dicynodonts, especially of the postorbital behind the postorbital bar, makes such an arrangement very probable. Crompton & Hotton (1967) have indicated the dorsal surface of the dentary and, possibly, surangular as the main insertion areas of this muscle, and suggest that a portion may have extended a short way down the medial side of the mandible.

Of interest in this connection is the fact that in *Cistecephalus*, *Cistecephaloides* and (judging by Cox's 1972 illustrations) *Kawingasaurus*, the dorsum of the dentary is bowed out laterally and the inner surface, together with that of the surangular, moulded to form a wide, shallow trough leading down to the exposed Meckelian sulcus. The sulcus, bounded by prearticular and splenial medially and angular and dentary laterally, is in a position equivalent to the opening described as the adductor fossa by Romer (1956) in reptiles, and which is primitively the major insertion area of the external jaw adductor muscles. The condition in cistecephalids can, it appears, be best explained in terms of a fairly substantial slip of the medial external adductor muscle inserting on the bones surrounding the Meckelian sulcus in dicynodonts, while in dicynodonts with narrow or medium-width intertemporal regions this adductor fossa would be an easily accessible insertion area for such a muscle, in cistecephalids the inner surfaces of the dentary and surangular above the sulcus and mandibular fenestra would inevitably have been influenced by the lateral migration of the muscle's temporal area of origin, and the course of the fibres is thus more clearly shown in them than in other dicynodonts.

Thus reconstructed, three sets of external adductor muscles appear to have inserted on the mandible in cistecephalids and presumably in other dicynodonts as well. An inner division of the medial external adductor muscle inserted in the adductor fossa, while, as reconstructed in dicynodonts by Crompton & Hotton (1967) and Cluver (1970, 1971), a lateral division of the medial external adductor muscle inserted on the dorsal dentary surface. (In *Cistecephaloides* this surface is slightly excavated to receive the muscle's insertion.) On the outer side of the dentary a lateral dentary shelf is developed in *Cistecephalus* and *Cistecephaloides*, and the lateral external adductor muscle would have inserted here. Cox (1972) does not mention a dentary shelf in *Kawingasaurus*, and the muscle would presumably have inserted on the outer side of the dentary, as suggested for *Dicynodon testudirostris* by Cluver (1970).

The effect of widening of the skull roof in cistecephalids would, it seems, have resulted in an overall lateral shift of the areas of origin of the external adductor muscles relative to their areas of insertion. A result of this would be increased control by these muscles over any lateral movement of the mandible across the palate. Indications that such movement was in fact possible are provided in the structure of the palate and the mandible, which differ in important respects from the condition in other dicynodonts. Among forms in which the jaw musculature and jaw movements have been reconstructed

Emydops (Crompton & Hotton 1967) could have utilized only a straightforward anteroposterior displacement during the masticatory stroke, guided by adjacent rows of upper and lower postcanine teeth, while a step in front of the articulation surface of the articular condyle prevented excessive sliding over the quadrate. In *Lystrosaurus* (Crompton & Hotton 1967; Cluver 1971) the anterior symphyseal region of the lower jaw was guided by the tight-fitting tusks, caniniform processes and palatal rim, and the quadrate and articular surfaces are closely-matched counterparts which appose any tendency for lateral displacement during the jaw movements. In a third group, represented by *Dicynodon testudirostris* (Cluver 1970), strongly developed caniniform flanges act as lower jaw guides, and enlarged crushing areas on the dorsal surface of the dentary meet apposing surfaces on the palate. In effect, in all these forms the dentary is so controlled as to meet specific areas of the palate during each masticatory stroke.

In cistecephalids, on the other hand, no such restrictions on the mandibular movements appear to be developed. The articular surface of the quadrate has two rounded condyles, but they are not separated by a deep cleft as in *Emydops* or *Lystrosaurus*, and there is considerable freedom of movement between it and the articular bone. No bony step, such as is found in *Emydops*, is present in cistecephalids, and, in *Cistecephalus* at least, the articular surface continues from the articular itself on to the surangular (this area is not clearly preserved in *Cistecephaloides* or described in *Kawingasaurus*). Anteriorly, the palatal rim is low in *Cistecephalus* and *Cistecephaloides* and evidently almost absent in *Kawingasaurus*. In none of the genera is a proper caniniform process found. The palate itself is wider than the symphyseal region of the lower jaw, and no crushing dentary tables are developed to appose raised areas of the palate. A sharp, spade-like anterior termination of the lower jaw is found in *Cistecephalus* and *Cistecephaloides*, but in *Kawingasaurus* the mandible appears to have been blunt anteriorly. In *Cistecephalus* and *Cistecephaloides*, and possibly in *Kawingasaurus*, the mandible is too short to meet the anterior part of the palate in 'beak bite' (Crompton & Hotton 1967), while contact between mandible and the lateral palatal rim could not have been achieved without sideways movement of the lower jaw.

In brief, then, the possibility of controlled lateral movements of the lower jaw during the masticatory cycle cannot be ruled out in the three cistecephalid genera, and there is in fact some positive evidence to show that this type of movement did take place, and was associated with the broadening of the intertemporal region.

The broad, open and slightly convex occiput of cistecephalids, which contrasts sharply with the condition in other dicynodonts, might be considered next. The loss of the posterior flange of the squamosal, which served as part of the area of origin of the medial external adductor muscle in other dicynodonts, might have been associated with the roofing-over of the temporal region, whereby the root of the zygomatic part of the squamosal lies virtually within the

temporal vault. Alternatively, the shape of the occiput may well have been determined by changes in the neck musculature. Here comparison with recent mammals yields suggestive results. Among insectivores, inferences may be drawn from the skull of the Cape Golden Mole (*Chrysochloris asiatica*). In this fossorial form the rounded occipital region, lacking pronounced occipital and sagittal crests, is reminiscent of the condition in cistecephalids, and has evidently been strongly influenced by development of the powerful neck and shoulder muscles (Dobson 1882) required for its digging and burrowing way of life. Gregory (1951) discussed the muscular and osteological adaptations in a number of insectivores, including the Oligocene *Apternodus*, where a special squamosal flange in the temporal region served to accommodate forwardly extended neck and forelimb muscles.

Direct and detailed comparisons between dicynodonts and fossorial mammals must inevitably be undertaken with caution, but it is tempting to link the insectivore-like occiput in cistecephalids with the digging adaptations in the forelimb of *Kawingasaurus*, described by Cox (1972). The manus in *Kawingasaurus* is unfortunately not known, but if the fused and elongated distal phalanges of two digits of the hand in *Cistecephalus* are taken into consideration, together with evidence of adaptations for skull strengthening and reinforcement in all three cistecephalid genera, then it seems reasonable to suggest that an at least semi-fossorial mode of life was generally selected for in the family. That this direction of specialization was accompanied by basic changes in mastication is suggested by the unusual palate–mandible relationships and the changed orientation of the medial division of the external jaw adductor muscles. However, differences between the palate and mandible of *Kawingasaurus* on the one hand and *Cistecephalus* and *Cistecephaloides* on the other show that more than one type of feeding activity was developed within this adaptive framework. While the varying degree of commitment to digging and perhaps burrowing activities in the three genera can be determined only when the postcranial skeleton of each group becomes better known, it does seem that the sharp, shovel-shaped jaw symphysis of *Cistecephaloides*, and to an extent *Cistecephalus*, indicates dietary preferences quite different to those of the possibly carnivorous *Kawingasaurus*, which (Cox 1972) may have dug for small, mudflat-dwelling invertebrates.

Summary

The skull and mandible of a new dicynodont genus are described and figured. It is concluded that the new form, for which the name *Cistecephaloides boonstrai* is proposed, is closely allied to *Cistecephalus* and the newly established *Kawingasaurus* (Cox 1972) and that a family, Cistecephalidae, should be retained to include these three genera. *Cistecephaloides* is unusual in the small size of the orbits, the prefrontal-postorbital contact, and the separation of the pterygoids in the ventral midline, with consequent incomplete closure of the interptery-

goidal vacuity. Comparisons between the three cistecephalid genera indicate the possibility of parallel evolution, and it is suggested that digging and perhaps burrowing activities were characteristic of this family, and could account for the specializations encountered in the group.

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Abbreviations

ang.	— angular	nas.	— nasal
art.	— articular	op.	— opisthotic
bas.	— basisphenoid	os.	— orbitosphenoid
boc.	— basioccipital	pa.	— parietal
den.	— dentary	pal.	— palatine
ect.	— ectopterygoid	par.	— prearticular
eoc.	— exoccipital	pas. r.	— parasphenoid rostrum
ept.	— epipterygoid	pfr.	— prefrontal
fr.	— frontal	pm.	— premaxilla
i.c.a.	— foramen for internal carotid artery	po.	— postorbital
		pro.	— prootic
ip.	— interparietal	prs.	— presphenoid
ipt.vac.	interpterygoidal vacuity	pt.	— pterygoid
jug.	— jugal	pt.f.	— posttemporal fenestra
jug. for.	— jugular foramen	q.	— quadrate
lac.	— lacrimal	qj.	— quadratojugal
lac.for.	— lacrimal foramen	soc.	— supraoccipital
lat.den.l.	— lateral dentary ledge	smx.	— septomaxilla
lat.pal.for.	— lateral palatal foramen	spl.	— splenial
lat.r.	— lateral ridge on dentary	sq.	— squamosal
max.	— maxilla	st.	— stapes
med. r.	— medial ridge on dentary	vo.	— vomer